ISOZYME VARIATION, ECOLOGY AND PHYTOGEOGRAPHY OF *ANTENNARIA SOLICEPS* (ASTERACEAE: INULEAE), AN ALPINE APOMICT FROM THE SPRING MOUNTAINS, NEVADA

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ABSTRACT

Antennaria soliceps Blake is a narrow endemic, known only from a small area of the Spring Mountains, Clark County, southern Nevada. The Spring Mountains are an isolated biome harboring many endemics, including *A. soliceps*. Populations of *A. soliceps* are found on a limestone talus ridge, which extends both above and below treeline for six km east southeast of Charleston Peak. This duodecaploid species is gynoecious, and reproduction is achieved through agamospermy and stoloniferous growth. Enzyme electrophoresis was used to assess the genetic diversity of five populations surveyed at one-mile intervals along the ridge. It appears that *A. soliceps* possesses only one electrophoretic genotype and, therefore, is a single genetic individual. *Antennaria soliceps* is hypothesized to be related to *A. aromatica* on the basis of habitat and morphological characteristics and to *A. parvifolia* on the basis of cytological and other morphological features. Establishment of *A. soliceps* probably occurred in the Pleistocene during which moister and cooler conditions allowed the migration of northern plant taxa to this area.

The Spring Mountains of southern Nevada are an isolated range occurring at the southern edge of the Great Basin. Clokey (1951), author of the first and only flora of the range, referred to them as the Charleston Mountains. Charleston Peak is the only summit of the range that rises above treeline. The range is surrounded by desert which acts as a barrier to alpine plant migration between mountain ranges in the Great Basin (Harper et al. 1978). The isolation of the alpine peaks of the Spring Mountains provided a unique environment in which several insular endemics evolved, including *Antennaria soliceps.*

Antennaria soliceps is a perennial herb characterized by a monocephalous flowering stalk and a cushion plant growth form. Its six-kilometer long range is restricted to the talus areas of a ridge, composed entirely of Mississippian limestone (Clokey 1951), both above and below treeline between Griffith and Charleston Peaks (Fig. 1). Although the genus is dioecious, only pistillate plants of *A. soliceps* are known to exist. As in other gynoecious species of *Antennaria* (Bayer 1990b), reproduction in *A. soliceps* involves gametophytic apomixis, as well as vegetative asexuality via stolons, resulting in the production of progeny that are genetically identical to the ma-

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ternal individuals. Thus, a low level of genetic diversity might be expected in the species. *Antennaria soliceps* has a very high ploidal level, and although an exact chromosome number has been elusive due to the high number of chromosomes, it has been observed that $2n$=ca. 168, making the species a duodecaploid (Bayer unpublished data) based on $x = 14$. This is the highest ploidal level recorded for any species of *Antennaria.*

Determining the origin of *A. soliceps* is problematical, as has been determining the phylogenetic relationships of several of the other high elevation endemics of the Spring Mountains, such as *Ivesia cryptocaulis* and *Tanacetum compactum* (Clokey 1951). In his protologue, Blake (1938) stated that *A. soliceps* belonged to the "*A. media* group", but was unique in possessing single large heads. Later authors (Clokey 1951; Knight 1990) echoed Blake's (1938) statements on the relationship. As in other agamic complexes, it is well documented that asexual *Antennaria* species are derived from sexual species (Bayer 1987), therefore we must look to a sexual species for the parents of *A. soliceps. Antennaria media* Greene and *A. pulchella* Greene (the diploid parent of *A. media*) resemble *A. soliceps* in being alpine plants with dark black or brown colored phyllaries, but they are polycephalous, do not develop the dense cushion plant growth form, and are not confined edaphically to limestone substrates (Bayer 1990a). Their leaf shape is linear-spathulate rather than cuneate-spathulate as in *A. soliceps.* However, *A. aromatica* Evert, a recently described (Evert 1984) sexual species from Montana and Wyoming, and *A. parvifolia* Nutt. (=*A. aprica* Greene sensu Clokey 1951) are two species that possess morphological, cytological, and ecological features that implicate them as the possible progenitors of *A. soliceps.* No other sexual species of *Antennaria* possesses characteristics that would involve them in the parentage of *A. soliceps.*

With the increased interest in genetic diversity of geographically restricted endemics and their conservation (Karron 1987), as well as the increased interest in genetic variation in clonal organisms (Ellstrand and Roose 1987), it seemed appropriate to investigate the genetic diversity in *A. soliceps.* An electrophoretic survey was therefore undertaken to determine genetic (clonal) diversity in this geographically restricted endemic. The study also discusses the origin and phytogeographic history of *A. soliceps* through morphological and ecological comparisons.

Methods

Location of sites and sampling. Antennaria soliceps occurs in scattered populations ranging from a few individuals to many hundred individuals. The Spring Mountains have been extensively botanized by well-known collectors, including Clokey, Alexander and Kellogg,

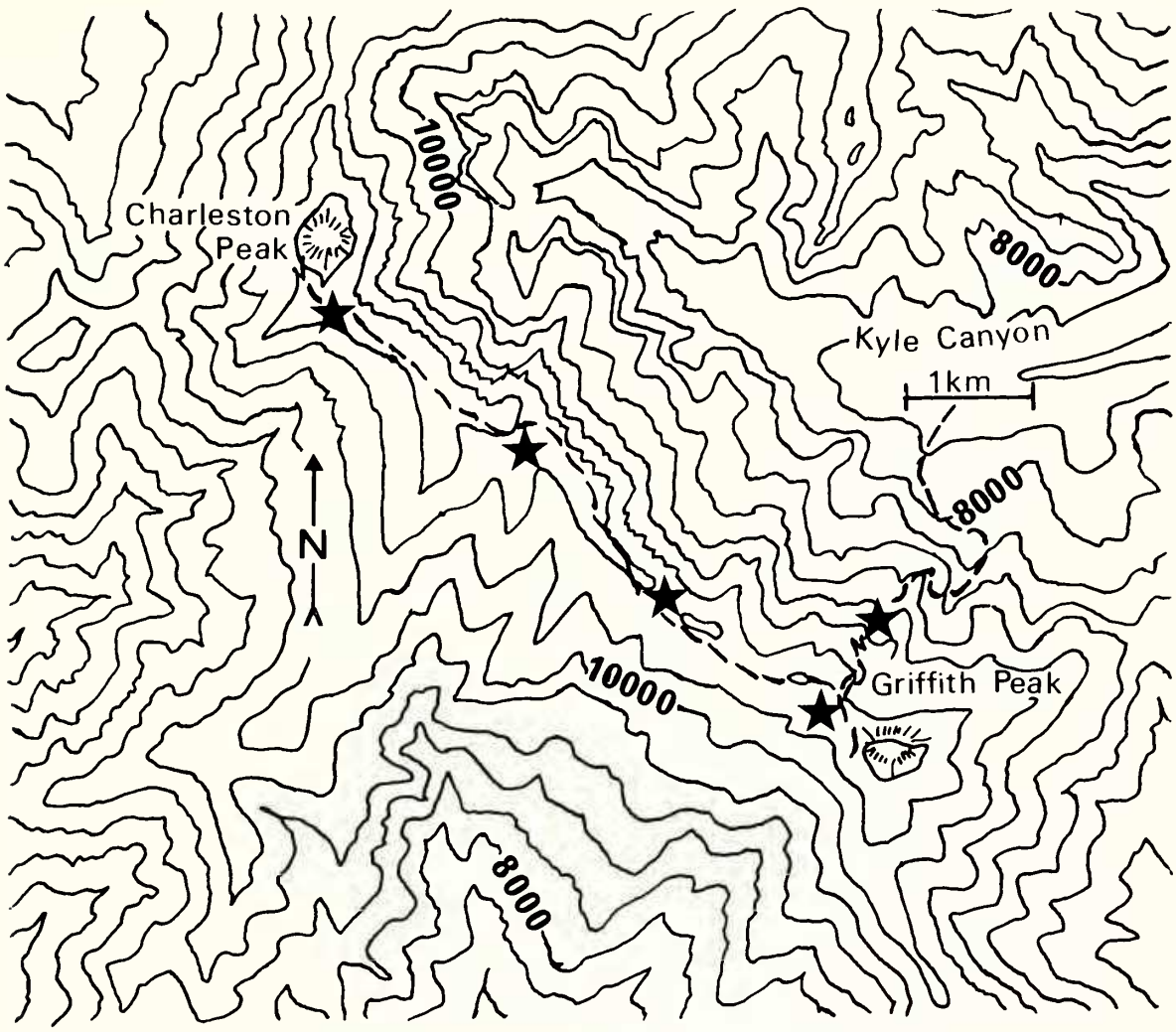

FIG. 1. Topographic map of the Charleston Peaks portion of the Spring Mountains, Clark Co., Nevada (contour interval = 400 ft). A prominent feature is the ridge extending between Griffith Peak (11,072′) and Charleston Peak (11,918′). Kyle Canyon is the location of the trailhead (7600′) of the "south loop" trail (dotted line). Populations of *A. soliceps* that were sampled (stars) occurred near treeline at elevations from 10,000′ to 11,150′ (3200–3400 m). Population identifications are from left (west) to right (on the north slope of Griffith Peak): NV-90020, NV-90019, NV-90018, NV-90017, and NV-700. Only sites NV-90020 and NV-90019 are truly alpine. Voucher specimens are at ALTA.

Train, Jones, Heller, Tidestrom, Hitchcock, and Jaeger among others (Clokey 1951) during the past 70 years, yet no additional sites for *A. soliceps* have ever been discovered. Recent explorations, targeting conservation of the species, have not uncovered any new sites (Knight 1990; T. Knight personal communication). In this study, four relatively large populations, covering the entire known range of the species, were sampled at equal intervals (about 1 mile apart) along the isolated ridge where *A. soliceps* occurs (Fig. 1). In addition, one rather ecologically atypical population, which occurs in the forest of bristlecone pine on the slope above Kyle Canyon, was also located and sampled (Fig. 1). Small portions of clones (ramets) were sampled at random and excavated for cultivation in the greenhouse.

Population genetics. Gel electrophoresis was carried out on 108 individuals from the five populations to determine the genetic diversity of the species. Nine enzyme systems were assayed: esterase (EST), glutamate oxaloacetate transaminase (GOT), leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), triosephosphate isomerase (TPI), acid phosphatase (ACP), malate dehydrogenase (MDH), phosphoglucomutase (PGM), and shikimic dehydrogenase (SKDH). Enzymes for assay were obtained from young leaves ground in cold Tris-HCl grinding buffer: 0.1 M Tris-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 0.2 M sucrose, 0.6% polyvinyl-polypyrrolidone (5:1 ratio of 40K: 360K m.w.), 2.0% PEG (8K m.w.), 0.1% BSA, and 0.002 M ascorbic acid. These extracts were then absorbed onto filter paper wicks and stored at −20°C overnight. The next day the wicks were loaded onto 12% starch gels and subsequently assayed for the above-mentioned nine enzyme systems. ACP, MDH, PGM, and SKDH were all observed using the same buffer system: the electrode buffer consisted of 0.007 M citric acid·H_2O and 0.065 M L-histidine (free base), and the gel buffer of 0.002 M citric acid·H_2O (pH 6.5) and 0.015 M L-histidine (free base) (Cardy et al. 1981). EST, GOT, LAP, PGI, and TPI were resolved using 0.038 M lithium hydroxide·H_2O–0.188 M boric acid (pH 8.3) as an electrode buffer and a gel buffer composed of 1 part 0.038 M lithium hydroxide·H_2O–0.188 M boric acid (pH 8.3), and 9 parts of 0.045 M Tris–0.007 citric acid (pH 8.4) (Soltis et al. 1983). The protocols described by Soltis et al. (1983) were used for staining the gels for each enzyme system.

The genetic basis of the isozyme banding patterns cannot be determined because of the high ploidal level of this taxon. Specifically, allelic frequencies for polymorphic loci lead to a large number of possible types of unbalanced heterozygotes, which cannot be visually differentiated in the gels [see Bayer (1989a) for a discussion of the problems associated with multisomic inheritance in *Antennaria*]. Therefore, a simple comparison of the banding patterns was carried out, and inferences were made based on the degree of similarity. Intensity of allozyme activity, banding patterns, and enzyme migration were characteristics on which the comparisons were based. Isozymes cannot be used to evaluate the origin of *A. soliceps* because of the uncertainty of genetic interpretation of the bands and because two possible parents, *A. aromatica* and *A. media,* do not have diagnostic alleles that can be used to confirm their presence in polyploid derivatives (Bayer 1989c). The isozymes of *A. parvifolia* have not been investigated, but high ploidy in this species complex would also hinder interpretation of the banding patterns, making use of isozymes as genetic markers difficult.

Ecology and morphology. An ecological study of *A. soliceps* was carried out using data on both the environment and community associates to compare the habitat of this species with one of its putative progenitors, *A. aromatica,* with which it appears to be very similar edaphically. Documentation of a similarity in habitat between the two species would lend additional support to our hypothesis that the two are a progenitor-derivative species pair. The methods were basically the same as those outlined in an earlier study (Bayer et al. 1991) and the data for habitats of *A. aromatica* were extracted from that earlier data set. At each *A. soliceps* study site, elevation above sea level (meters) and slope (degrees) were measured using a calibrated barometer and clinometer, respectively. Soil temperature difference (°C) between the surface and 10 cm depth, and soil unconfined strength (kg/cm^2), measured by a soil penetrometer, were recorded. This gives a measure of the insulating/temperature retention capacity of the soil.

Soil samples were collected from each of the five study sites, allowed to air dry, and subjected to chemical analysis by the soil analysis laboratory at the Northern Alberta Forestry Center, Edmonton. The macro- and micronutrients measured include extractable forms of calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (PO_4), potassium (K), sodium (Na), sulfur (SO_4), and zinc (Zn) measured in mg/kg. Nitrogen was not determined, as the amount of this nutrient often varies between the time the soil is collected and the time of analysis. The percent organic matter and pH of the soil were also determined. Herbarium specimens of all community associates were also collected from each site and were identified using taxonomic keys in Clokey (1951). The nomenclature (Table 1) follows Clokey (1951), as more recent floristic treatments do not exist for southern Nevada.

Ordination of nominal species data and environmental variables from thirteen study sites (five of *A. soliceps* and eight of *A. aromatica*) was carried out using the canonical correspondence analysis (CCA) option of the Canonical Community Ordination (CANOCO) program (ter Braak 1985). This method of analysis allows the environmental variables to be related to species data simultaneously and is becoming the preferred ordination method for the analysis of data used in vegetation classification (ter Braak 1986, 1987, 1988; John 1989; Gignac and Vitt 1990; Bayer et al. 1991). The program was run without any transformation of the variables, weighting environmental variables, or axis rescaling. In this study, the ordination was performed to determine and visualize the habitat and species associates for the two *Antennaria* species.

Gross morphological comparisons among species of *Antennaria*

TABLE 1. COMMUNITY ASSOCIATES FROM FIVE SITES CONTAINING POPULATIONS OF *ANTENNARIA SOLICEPS*. Presented are taxon names arranged alphabetically by genus and occurrence (+ = present; − = absent) at each of the sites; 07 = NV-700, 17 = NV-90017, 18 = NV-90018, 19 = NV-90019, 20 = NV-90020; * = endemic to Clark Co., Nevada (Spring Mountains and adjacent Sheep Range, ** = endemic to the Spring Mountains, *** = narrowly endemic to the Charleston Peak area and ridges extending from it. All other taxa are more widespread in North America.

Taxa	Sites				
	07	17	18	19	20
Actinea lemmonii (Greene) Blake	−	+	+	+	−
Antennaria soliceps Blake***	+	+	+	+	+
Aquilegia scopulorum Tidestr.	−	+	−	−	−
Artemisia michauxiana Besser	−	+	−	−	−
Astragalus mancus (Rydb.) Wheeler	−	+	+	−	−
Astragalus platytropis Gray	−	−	−	−	+
Crepis nana Richards.	−	−	−	−	+
Cystopteris fragilis (L.) Bernh.	+	−	−	−	−
Dodecatheon jeffreyi Moore var. *redolens* Hall	−	−	−	+	−
Draba jaegeri Munz & Johnston *in* Munz***	−	−	−	+	+
Erigeron clokeyi Cronquist	−	+	+	+	+
Erysimum capitata (Dougl.) Greene	+	−	−	−	−
Festuca ovina L. var. *brachyphylla* (Schult.) Hall	−	−	−	+	−
Gutierrezia sarothrae (Pursh) Britton & Rusby	−	+	−	−	−
Ivesia cryptocaulis (Clokey) Keck***	−	−	−	+	+
Jamesia americana Torr. & Gray	+	−	−	−	−
Lesquerella hitchcockii Munz*	−	+	−	+	+
Lupinus alpestris A. Nels.	+	−	−	−	−
Oenothera caespitosa Nutt. var. *crinata* (Rydb.) Munz	−	−	−	−	+
Oxytropis oreophila Gray	−	+	−	+	+
Pedicularis semibarbata Gray ssp. *charlestonensis* (Pennell & Clokey) Clokey*	+	−	+	−	−
Penstemon keckii Clokey**	+	−	−	−	−
Physaria chambersii Rollins	+	−	−	−	−
Pinus longaeva D. K. Bailey (*P. aristata* of Clokey)	+	+	+	+	−
Poa secunda Presl.	−	−	+	−	−
Potentilla beanii Clokey***	−	+	+	−	−
Ribes montigenum McClatchie	−	−	−	+	−
Sitanion hystrix (Nutt.) Smith	−	+	−	+	+
Tanacetum compactum Hall***	−	−	−	+	+
Trisetum spicatum (L.) Richt.	−	−	+	−	−
Valeriana puberulenta Rydb.	+	−	−	−	−

were based on examination of herbarium material at ALTA and cultivated living material.

RESULTS

All nine enzyme systems produced favorable enzyme activity and good resolution. Variation among the 108 individuals assayed was

FIG. 2. Gross morphological comparison of *Antennaria parvifolia* (left), *A. soliceps* (center) and *A. aromatica* (right). These pistillate specimens are from populations CO-90053, NV-90020, and M-628 for *A. parvifolia, A. soliceps* and *A. aromatica,* respectively. Vouchers at ALTA.

absent, as banding patterns and staining intensity were identical in all individuals for the nine enzyme systems.

Antennaria soliceps and *A. aromatica* have similar morphology. The overall size of the plants (Fig. 2) is similar as is their cushion plant growth form. Leaf size, shape, and spacing on the short stolons are similar in both species (Fig. 2). Head size is somewhat comparable, but with respect to head number per stem *A. aromatica* is pleiocephalous and *A. soliceps* usually monocephalous (Fig. 2). Both possess brown or green-based phyllaries with white or brown at the tips. The typical habitat of *A. soliceps* is calcareous talus at an elevation equal to or above treeline, as is that of *A. aromatica* (Bayer 1989b). The comparisons of gross morphological features between *A. soliceps* and *A. aromatica* (Fig. 2) suggest that the two species are closely related and that *A. aromatica* may be a parental species of *A. soliceps.* In its large head size and more spathulate leaf shape, *A. soliceps* also resembles *A. parvifolia,* whose sexual phase still occurs on montane slopes in the Spring Mountains at elevations up to 3150 m.

In the ordination diagram (Fig. 3), the lines representing environmental variables point in the direction of maximum change in the variable, and the length of the line indicates a relative measure of the rate of change in that variable (ter Braak 1987). Therefore, longer lines, especially those that extend to the margin of the graph, are more important parameters than short ones and tend to be more closely related to the patterns of community variation (ter Braak 1987). The relative position of each *Antennaria* species site or each community associate can best be viewed by projecting the points onto the lines. This is accomplished by first extending each line,

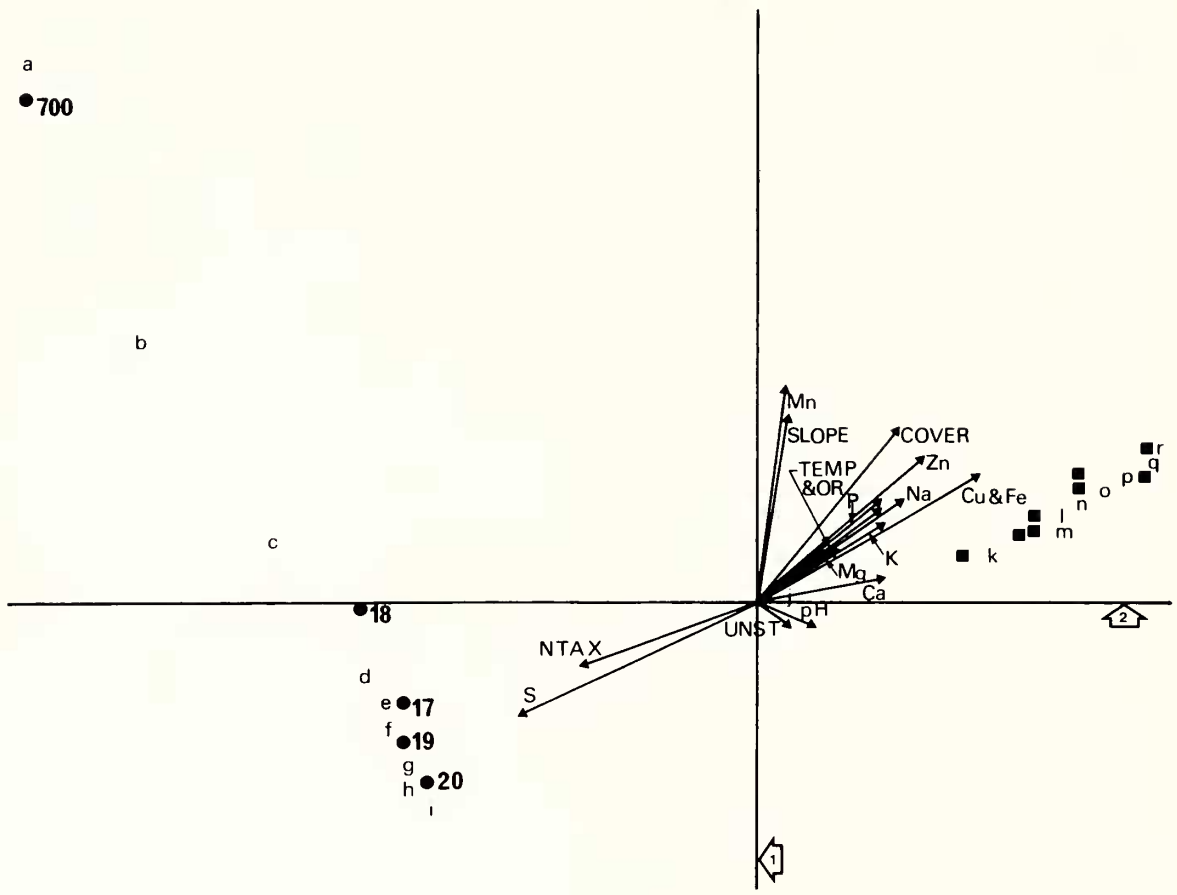

FIG. 3. The distribution of five study sites of *Antennaria soliceps* (solid circles) and eight of *A. aromatica* (solid squares) along CCA ordination axes 1 and 2 with environmental variables indicated by arrows. See text for guidance in interpretation of this diagram. Environmental factor abbreviations are as follows: Extractable forms of calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (P), potassium (K), sodium (Na), sulfur (S) and zinc (Zn) and percent organic matter (OR), soil temp (TEMP), percent cover (COVER), slope (SLOPE), pH (pH), number of taxa at each site (NTAX), and soil unconfined strength (UNST). Site abbreviations for *A. soliceps* are NV-700 (700), NV-90017 (17), NV-90018 (18), NV-90019 (19), and NV-90020 (20). Community associates are represented on the ordination axes as lower case letters. Several species may be represented by one letter and abbreviations are as follows: a = *Cystopteris fragilis, Erysimum capitata, Jamesia americana, Lupinus alpestris, Penstemon keckii, Physaria chambersii,* and *Valeriana puberulenta,* b = *Pedicularis semibarbata* ssp. *charlestonensis,* c = *Pinus longaeva,* d = *Astragalus mancus* and *Potentilla beanii,* e = *Actinea lemmonii,* f = *Aquilegia scopulorum, Artemisia michauxiana, Erigeron clokeyi* and *Gutierrezia sarothrae,* g = *Dodecatheon jeffreyi* var. *redolens, Lesquerella hitchcockii, Oxytropis oreophila,* and *Ribes montigenum,* h = *Draba jaegeri, Ivesia cryptocaulis,* and *Tanacetum compactum,* i = *Astragalus platytropis, Crepis nana* and *Oenothera caespitosa* var. *crinata,* j = grasses, k = *Paronychia sessiliflora, Pteryxia hendersonii,* and *Ribes inerme,* l = *Antennaria umbrinella* and *Astragalus alpinus,* m = *Androsace chamaejasme, Arcostaphylos uvi-ursi, Dryas octopetala, Hedysarum alpinum, Valeriana edulis, Astragalus aboriginum* and *Oxytropis campestris,* n = *Potentilla pensylvanica* and *Zygadenus elegans,* o = *Pentaphylloides floribunda, Erigeron ochroleucus, Lupinus argenteus, Oxytropis splendens, Silene acaulis, Geum rossii* and *Minuartia obtusiloba,* p = *Senecio canus, Phlox caespitosa* and *Anemone multifida,* q = *Bupleurum americanum, Draba oligosperma, Eritrichium nanum* and *Hymenoxys acaulis,* r = *Ivesia gordonii* and *Penstemon attenuatus.*

TABLE 2. SOIL COMPOSITION AND ENVIRONMENTAL VARIABLES FROM FIVE SITES CONTAINING *ANTENNARIA SOLICEPS*. Presented are minerals, percentage organic matter, pH, soil temperature difference between the surface and 10 cm depth (STEMP), unconfined soil strength (UNSTR), slope and percentage cover. Site abbreviations: 07 = NV-700, 17 = NV-90017, 18 = NV-90018, 19 = NV-90019, 20 = NV-90020.

Soil/plant components	Sites				
	07	17	18	19	20
Calcium (mg/kg)	254.2	355.9	614.8	516.3	588.6
Copper (mg/kg)	0.07	0.09	0.45	0.06	0.25
Iron (mg/kg)	0.9	0.11	0.84	0.30	0.47
Magnesium (mg/kg)	56.83	91.17	293.6	131.0	134.0
Manganese (mg/kg)	13.21	5.56	7.46	4.29	2.80
Phosphorus (mg/kg)	1.11	0.73	1.02	1.47	2.07
Potassium (mg/kg)	115.2	103.4	184.2	111.2	135.5
Sodium (mg/kg)	5.29	7.60	15.61	10.48	15.70
Sulfur (mg/kg)	18.99	23.87	52.80	40.18	53.18
Zinc (mg/kg)	0.45	0.01	0.01	0.01	0.01
Organic matter (%)	2.48	1.90	4.87	1.69	4.49
pH	6.9	7.28	7.56	7.46	7.55
STEMP (degrees C)	3.0	4.0	1.0	2.0	4.0
UNSTR (kg/cm^2)	1.50	1.75	1.5	2.0	2.5
Slope (degrees)	1.0	0.5	0.5	1.0	1.5
Percentage cover	30.0	20.0	25.0	18.0	18.0

either on paper or in the mind, in both directions to the edge of the diagram. Then draw or visualize a line from the site symbols, perpendicular to the line until it intersects the line. The ranking of those endpoints along the line is an approximate indication of the relative value of the weighted average of each species site with respect to that environmental variable. Also, the origin of the line indicates the grand mean, therefore if the endpoint of the line lies on the same side of the origin as the perpendicular intersect then that site has a weighted average that is higher than the grand average and vice-versa (ter Braak 1986). The raw environmental data are presented in Table 2.

From Figure 3 we can deduce that although *A. aromatica* and *A. soliceps* have distinct habitats, most of the environmental factors are not very different between their sites because the arrows are all relatively short in length. This is especially true if we compare these results to habitat differentiation between *A. aromatica* and other western North American species of *Antennaria* (Bayer et al. 1991), where all of the sexual taxa investigated differed by relatively large environmental differences. However, *A. aromatica* sites tend to differ from the *A. soliceps* sites by having relatively higher amounts of cover, zinc, sodium, copper, iron, and phosphorus in the soil and lower amounts of sulfur and numbers of species associates (NTAX) at the sites. Although copper, manganese, sulfur, and zinc may be

toxic to plants at certain pH values, it is unlikely that any of these nutrients affect the growth of the plants at the *A. soliceps* sites because the pH values of the soils are neutral to slightly alkaline and the amounts of all of these nutrients are at the low end of the range in amounts of these nutrients that are found in soils in general (Table 2). No community associates are shared by the two sets of sites, except the broad category of grasses (j), as might be expected due to the great phytogeographic distance that separates the range of the two species. The *A. aromatica* sites are all remarkably similar to each other and differ primarily by the above-mentioned environmental factors as well as having different species associates at each site (Fig. 3). The typical sites of *A. soliceps* that occur on the top of the ridge are also fairly similar to each other (Fig. 3). The atypical site (NV-700), which occurred well below treeline below site NV-90017, was quite different from the other sites (Fig. 3). Site NV-700 was most different from the other *A. soliceps* sites because it occurred on a slightly steeper slope with soil much higher in manganese than the other sites. Also this site had a completely different set of species associates including *Cystopteris fragilis, Erysimum capitata, Jamesia americana, Lupinus alpestris, Penstemon keckii, Physaria chambersii,* and *Valeriana puberulenta,* only sharing *Pedicularis semibarbata* and *Pinus longaeva* with the other sites (Fig. 3). Compared to edaphic conditions for other species of *Antennaria* (Bayer et al. 1991), *A. aromatica* and *A. soliceps* are more similar to each other than to other species of *Antennaria* because the sites of these species have gravelly soils, with high amounts of calcium, sulfur, and low manganese (Mn) and are found at high elevations in full sun.

Discussion

Population genetics. A lack of genetic variation in the nine enzyme systems among 108 individuals strongly suggests that the entire species is a single genotype. This absence of genetic diversity is completely concordant with our supposition that *A. soliceps* is a gametophytic apomict, producing progeny that are genetically identical to the parental individuals. *Antennaria soliceps* thus apparently arose as a single pistillate individual that established itself on the Spring Mountains and reproduced apomictically. If more than one clone of *A. soliceps* did arise at the time of its origin, then its tiny geographic range could have resulted in the loss of all but one genotype. Consequently, the total lack of genetic variation within *A. soliceps* may be one explanation for its continued restricted range today, as there is no genetic variation that allows for individuals preadapted to slightly different environmental conditions to expand the range of the species. Additional explanations for its restricted range may relate to the dispersability of propagules to other suitable

habitats and their ease of establishment in those habitats. Because *A. soliceps* consists of a single genotype, its ability to survive changing climatic conditions will depend on the degree of phenotypic plasticity within this genotype.

Antennaria soliceps presents a somewhat unusual case when trying to compare its genetic population structure with that found in other plant species because it is not only a geographically restricted endemic, but is also an apomict. Karron (1987) summarized data on isozyme variation for widespread versus restricted congeneric species for all types of breeding systems, whereas Ellstrand and Roose (1987) reviewed that for clonal plants. Based on the data in these reviews it might be expected that a narrowly restricted agamospecies, such as *A. soliceps,* would have very small amounts of genetic variability and therefore it is not surprising to find that it is monoclonal. The only other species investigated thus far having a similar breeding system and somewhat narrow distribution is the gametophytic apomict, *Taraxacum obliquum* (Oostrum et al. 1985). No variation in genetic composition was detected in populations from the coast of the Netherlands, indicating that the populations were also monoclonal (Oostrum et al. 1985).

Phytogeography and evolution. The similarities between *A. aromatica* and *A. soliceps,* both the terms of morphology (Fig. 2) and habitat (Fig. 3), suggest it may be a parent. Growth form, leaf shape, phyllary color, and habitat are strikingly similar between the two taxa (Fig. 2). Unlike *A. aromatica, A. soliceps* is neither glandular nor aromatic, but neither are other apomicts thought to be derived from *A. aromatica* (Bayer 1989b). When *A. aromatica,* which occurs as a sexual species at diploid ($2n=28$) and tetraploid ($2n=56$) ploidal levels, is artificially hybridized with any other of a number of other sexual species of *Antennaria,* the resultant F_1 interspecific hybrids (vouchers at ALTA) are always non-glandular and odorless (Bayer unpublished data). Since most apomictic *Antennaria* are thought to be of allopolyploid (hybrid) origin (Bayer 1987), then *A. soliceps* is probably a hybrid between *A. aromatica* and some other sexual species of *Antennaria. Antennaria soliceps* also resembles *A. parvifolia* in its large head size and more spathulate leaf shape. Additional evidence in favor of *A. parvifolia* as contributing to the parentage of *A. soliceps* is cytological. *Antennaria soliceps* is high polyploid (ca. duodecaploid) and only in *A. parvifolia,* which occurs as a sexual species at tetraploid, hexaploid ($2n=84$), octoploid ($2n=112$) and decaploid ($2n=140$) ploidal levels, do ploidal levels approach that magnitude (Bayer and Stebbins 1987). The propensity for very high ploidal level in *A. soliceps* could have been inherited from *A. parvifolia.*

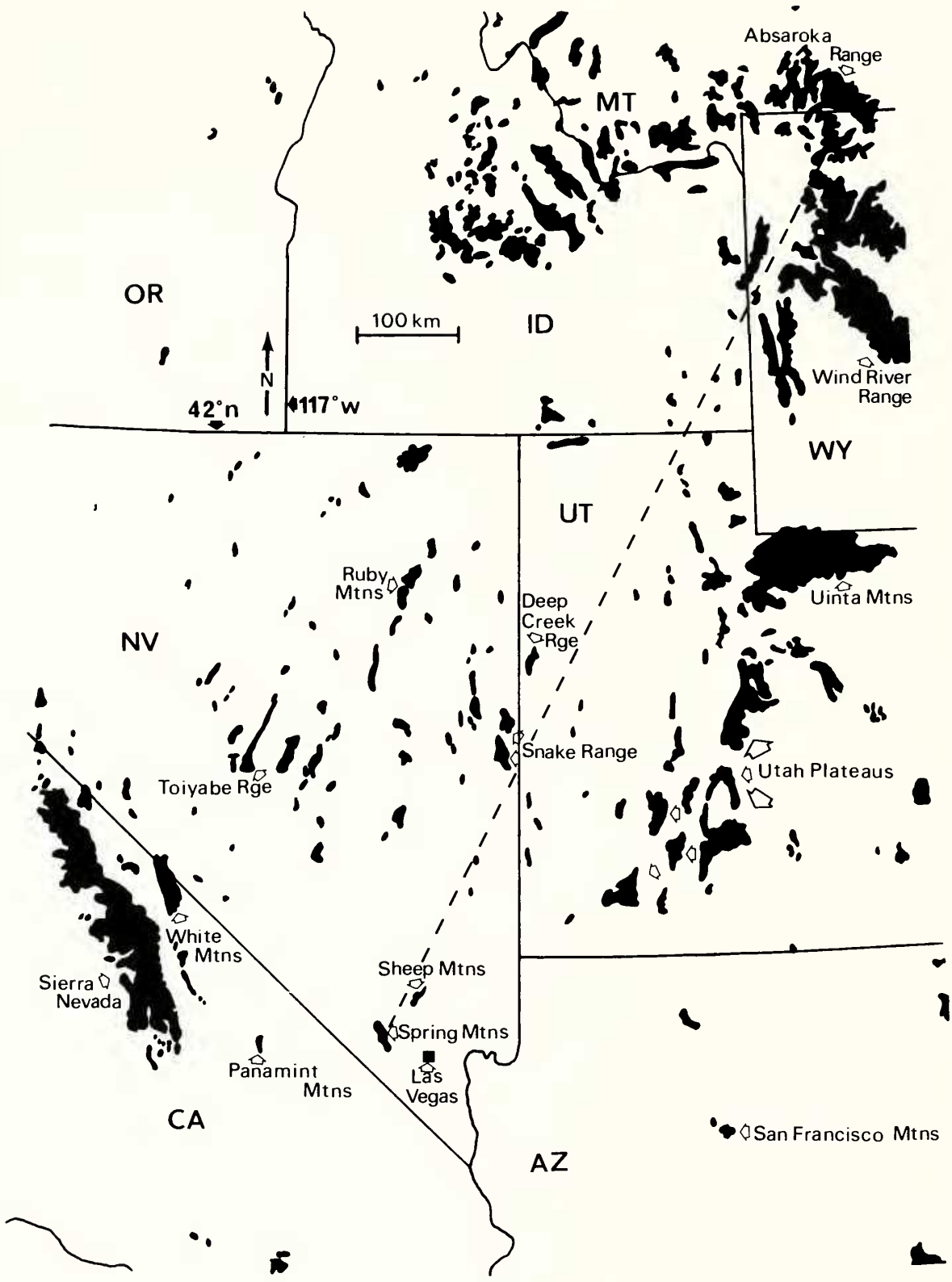

FIG. 4. Map of the Intermountain Region of the southwestern United States. *Antennaria soliceps* is endemic to the Spring Mountains. Areas in black are regions that are considered entirely or partially alpine at the present time (based on Billings 1978). Major mountain ranges are labeled. *Antennaria aromatic* occurs in the Absaroka Range, which is about 1000 km (dotted line) northeast of the Spring Mountains.

The flora of the Spring Mountains contains 12 endemics at high elevations from subalpine to alpine (Clokey 1951) and *A. soliceps* co-occurs with several of these including *Draba jaegeri, Ivesia cryptocaulis, Penstemon keckii, Potentilla beanii,* and *Tanacetum compactum* (Table 1). Billings (1978) has calculated an index of similarity between the Spring Mountains and other ranges of the Great Basin, Rockies and Sierra: Absaroka Range (8%), Deep Creek (13%), Ruby Mountains (8%), Toiyabe Range (18%), White Mountains (16%), Sierra Nevada (10%), and San Francisco Mountains (14%) (Fig. 4). Based on this, it is only about twice as likely that nearby mountain ranges (except the Ruby Mountains) are the source of the ancestors of *A. soliceps* as the distant northern Rockies (Beartooth Plateau; Absaroka Range) (Fig. 4). Also, overall the Rockies have had a much greater effect on the vascular plants species composition of mountains of the Great Basin than has the Sierra (Billings 1978). Additionally, the Rockies and Great Basin ranges have large areas of limestone talus habitat whereas the Sierra has very little (Billings 1978).

We offer the following phytogeographic hypothesis to account for the present day distributions of *A. aromatica* and *A. soliceps. Antennaria soliceps* may have established itself in the Spring Mountains during the Pleistocene when the continental climate was cooler and moister. During this epoch, the immediate area around the Spring Mountains was not desert as it is at present, rather there were many lakes and a diverse flora (Thompson and Mead 1982). Small glaciers existed on the peaks of the Spring Mountains creating cirques which now provide habitat for numerous endemics (Billings 1978). Alpine areas of Charleston Peak are much moister than the valley floor and lower slopes, but they are drier than comparable areas in the Rockies and Sierra Nevada because of the tremendous rainshadow provided by the Sierra (Billings 1978). Alpine habitat of the Charleston peak area was larger during the Quaternary (Fig. 4).

Perhaps *A. aromatica* expanded its range, during the Quaternary, towards the south and for a time occurred in southern Nevada (Fig. 4). Most of the ranges of eastern Nevada south of the Ruby Mountains are topped with calcareous rock, which could have provided "stepping stones" of suitable habitat for *A. aromatica* during the Pleistocene. If *A. aromatica* did occur in southern Nevada at that time, then it hybridized with another species of *Antennaria,* possibly *A. parvifolia,* giving rise to an asexual clone which established itself in the nearby mountains. As the climate became drier and warmer after the Pleistocene, this range became isolated from other mountain ranges by the newly-formed desert. This desert then acted as a substantial barrier to plant migration between the ranges of southern Nevada. Irrespective of the origin of this new asexual clone of *Antennaria,* i.e., *A. soliceps,* it was now left geographically isolated.

With the warming and drying which took place, *A. aromatica*'s range would also have decreased and again become restricted to Wyoming and Montana. Even though suitable habitat of proper elevation and characteristic limestone talus does exist in southern Wyoming and in Colorado, just south of *A. aromatica*'s current range, the species is not found growing here (Bayer 1989b).

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